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ONTOGENY IN EVOLUTION

By B. S. Matveyev

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FACTORS WHICH DETERMINE CHANGES OF ONTOGENY IN
EVOLUTION

by B.S. Matveyev*

[Following is a translation of a paper by
B.S. Matveyev entitled "Faktory, opredelyayu-
shchiye izmeneniya ontogeneza v evolyutsii"
(English version above) in Arkhiv Anatomii,
Gistologii i Embriologii (Archives of Anatomy,
Histology and Embryology), Vol. 38, No. 3,
1960, Leningrad, pages 3-15.)

At present interpretation is generally accepted
that neoplasms, determining the formation of new features
in evolution, arise during the entire individual develop-
ment, beginning with the conception of sex cells in parent
organism to the very death of the organism. This idea

* A.N. Severtsov Institute of Animal Morphology, AS,
USSR and Laboratory of Vertebrate Morphology, MGU.

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has been expressed by Darwin in his early essays on the origin of species, still in 1842 and 1844 and later repeated in "Origin of the Species" (1859). Then it was proved and developed by F. Muller in his book "On Darwin" (1864). However, later it was forgotten and replaced by the theory of Haeckel's biogenetic law. Haeckel defended another point of view in biogenetic law. According to Haeckel, ontogeny is a reflection of phylogeny, i.e., the neoplasms changing the structure and function of animals as adjustments to existence conditions, originate in adult animals, and later the acquired changes shift into embryologic condition, constantly replaced by new ones, in the subsequent generations. In spite of further criticism of biogenetic law, such an interpretation of factors, determining the recapitulation of ancestor characteristics in the ontogeny of descendants, established for a long time in biological literature.

A. N. Severtsov was one of the first who reintroduced the idea that evolution is accomplished by the changing ontogeny (1911-1912). However, A.N. Severtsov in the phylembryogenesis theory discussed only the origina-

tion in evolution of adult form characteristics and up to 1935 incorrectly interpreted the views of Darwin on this problem (B.S. Matveyev, 1940, 1946, 1948), comparing them to the views of F. Muller. Causal factors, determining the change in ontogeny, he did not touch upon, posing only the problem of when and how the changes of adult forms originate in phylogenetic development, or not why. Present theorists of the science of evolution discussing the role ontogeny transformations in the process of evolutionary development (G. deBeer 1930-1958, B. Rench 1954, A. Remane 1956), and also all Soviet biologists beginning with A.N. Severtsov, independently of Darwin revived the idea that evolution comes about by the way of changing the course of ontogeny, not discussing the problems of factors causing these changes. Ontogenetic factors are analyzed in detail in the experimental embryology, but the representatives of development mechanics do not relate their analysis of individual development factors with historic development process, analyzing only their physiological essence.

Later study of this problem by morphologists (A. Naef 1917; B. Frants 1927; G. deBeer 1930-1958;

I. Shmal'gauzen 1938, 1942 and 1948; B. Rensch 1954; A. Remane 1956) also are limited mainly by the establishment of different forms of phylogenetic transformations of individual development, paying much less attention to the problem of causes and factors. In the last summary on the given problem, B. Rensch (1954) said that the entire evolution is based exclusively on the mutations of "Penov" chromosomes, the entire genome or cytoplasm of embryonic cells. Along with these qualitative changes, quantitative changes are especially frequently met through acceleration or retardation of ontogenesis, separate ontogenetic phases or the development of separate organs or structures, through heterochrony. Further, he pays attention to the process of abbreviation and prolongation of ontogenesis and then lists eight different forms of these transformations, using as the basis A.N. Severtsov phylembryogenetic types. I.I. Shmal'gauzen gave main attention to internal developmental factors causing displacements in morphogenetic correlations, striving to attract the developmental mechanics to this problem. Some soviet morphologists (S. Kryzhanovskiy 1939-1957, V. Vasnetsov 1940-1953 and their pupils) and physiologists

I. A. Arshavskiy, developing the ecological embryology trend, reduce all ontogenetic transformations to straight adaptations in the developing embryo to the environment and deny the preservation of historic inheritance in embryos as remnants of the past, which do not accomplish the adjustment functions to the conditions of embryonic development.

In the Soviet Union at present with the study of ontogenetic evolution by method of comparative juxtaposition of close systematic animal groups, great amounts of material accumulated, which allows summation of the development of the problem of factors determining the change in ontogeny. A final solution of this problem cannot be given by comparative morphological studies; the participation of evolutionary physiologists, biochemists and geneticists is needed here, in order to explain the metabolism characteristics in different stages and periods of ontogeny. However, comparative ecolo-morphological studies of ontogeny for closely related animal groups (V. Vasnetsov, S. Kryzhanovskiy, B.S. Matveyev, G.A. Shmidt and their pupils) allowed division of the individual development of animals into periods and stages, character-

ized by special forms of adaptations to the change of habitat. This analysis of specific characteristics of organ structure and function in different periods and stages makes it possible to raise the problem on factors determining the change of ontogeny, which should aid physiologists, biochemists and geneticists to reach the experimental answer to the raised problems.

As was stated above, Darwin had already pointed out with definitive clearness in the essay of 1844, that "negligible changes initially appear in all life periods" and that "with inheritance they are inclined to appear again in the corresponding age" ("Essay 1884", Works, Vol. 3, 1939, page 226). These Darwinism ideas fully correspond to our present views on the origin of new adaptive characteristics with the divergence of features in the formation of species.

According to present views, they originate as ontogenetic changes in the gamut, beginning with the ovum and ending with the adult stage. Morphologic and physiologic features of adult animals, as definitive signs, have developed as adaptations to the habitat conditions of

the adult animals, providing their life and reproduction. In individual development each species in different periods and stages of their developmental possess specific adaptations to the conditions of embryonic and post-embryonic development. All principle functions of the life process (nutrition, breathing, excretion) in embryos and larvae are different than in adult organisms. Transformations of these specific embryonic and post-embryonic functions to the special conditions of life (different than in the adult organisms) are the source of enoplasms with the formation of species in adaptive evolution. In addition to this, structure and functions change, not only in embryo and larva, but also in the formation of features which change in adult animals. The character of these changes is extremely varied, and in genetically successive series of ontogenies (phylogenies) only those signs are conserved and strengthened by natural selection which are useful signs, which determine the survival of the best adapted to the given environmental conditions.

We can separate the factors, determining the changes in ontogenesis, into three categories:

1) Heterogeneity of hereditary structure and biochemical composition of maternal and paternal germ cells, which give beginning to daughter organism (cytoplasm and also deutoplasm).

2) Displacements in morphogenetic correlations with the establishment of organs, caused by different differentiation rates in embryonic cells and tissue functions, corresponding to the differences in their developmental conditions.

3) Function transformation in relation with the change of environment in different states and periods of individual development.

In analyzing these factors we should remember Darwin's statement: "In whatever period of life the new characteristic initially appears, it usually remains hidden in the descendant until it reaches the corresponding age, and then it develops. When this rule is not confirmed the cub usually develops the characteristic at an earlier age than the parents". ("Changes in domestic animals and developmental growth in domestic conditions", Works, Vol. 4, page 360).

We should remember, that in consequence of the

general asynchronous nature of individual development of different organs, there is no specific sequence in the development of these factors, each of them can develop at different times and, depending on the organisms, needs corresponding to the environment.

In the first place, the heterogeneity of hereditary structure and biochemical composition of maternal and paternal germ cells becomes effective in every daughter organism uniting in different combinations. This heterogeneity of hereditary structure of daughter and parent organism can tell on the different stages of ontogeny itself; it can change the entire ontogeny, and effect only separate specific signs. I will not touch upon these problems; these problems are beyond my scope, and this is a concern for geneticists and biochemists. Speaking on the influence of the factors on this order on ontogeny, I would like only to emphasize by a separate example, that not only heterogenous composition of the chromosome apparatus and cytoplasm can determine specific deviations in ontogeny, but also the compositional character of the pellicle in the ovum, i.e., the food material, received by the germ cell while it was still a part of the

maternal organism, of its gonad.

The principle ontogenetic stages are illustrated in Fig. 1 for two neighboring species of Black Sea labroid fishes (Labridae family) Grenilabrus and Ctenolabrus of the Order Perciformes. In spite of the great similarity in the habitat for adult fish, the course of their embryonic and post-embryonic development differs much from start to finish. The sizes of their ova are very similar, as are the adult forms: in Grenilabrus - 0.80 - 0.90 mm, in Ctenolabrus - 0.78 - 0.84 mm, but Ctenolabrus has a typical pelagic fish eggs with very thin membranes and transparent, colorless vitellicle of watery consistency. This vitellicle composition determines the entire ontogenetic course. In the cleavage stages the embryonic disc in Ctenolabrus is spread on to the vitellicle and the blastomers are not separated by a sharp boundary from the vitellicle. The hatching of larvae occurs very early and the larvae conducts a pelagic form of life, having a whole number of larva adaptations to the pelagic life. Grenilabrus has a bottom-dwelling type of ovum fixed to stones with very thick sticky concentrated vitellicle of bright yellow.

The ova membranes are very dense, thick and able to adhere. In the division stage the blastomers are isolated by a sharp boundary from the vitellicle in the form of a cap around the vitellicle. Hatching is very late, as the concentrated vitellicle provides the food for the embryo for a long time, and this in the littoral conditions of bottom dwelling ova is an important biological adaptation.

Consequently, the character of biochemical processes in the germ gland of the female, where the ovum of daughter organism is formed, determines all the subsequent ontogenetic course and sharp differences in the biology of development for these two closely-related species of fishes belonging to one family.

It should rather be said that the differences in vitellicle composition form a material for natural selection, giving it the possibility for the adaptation of these two fish species to different ecological conditions.

The second group of factors, influencing the morphogenetic course, are the displacements in the relationship of rudiment function, forming morphogenic systems,

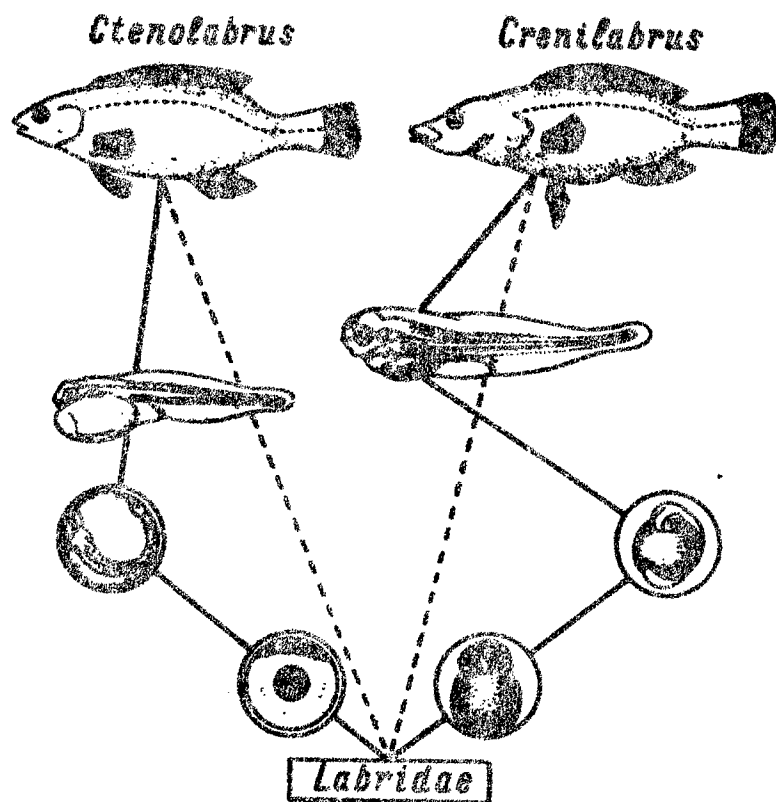


Fig. 1. Diversions of signs in the ontogenesis of the two fish species, *Crenilabrus* and *Ctenolabrus* from the family Labridae, caused by the different composition of their deutoplasm.

i.e., displacements in morphogenetic correlations between two rudiments, of which one played the role of formative action carrier (activator), and the other is the regulating material (reactor) on the morphogenic action of the activator. The study of mutual interaction of these morphogenetic systems or, as D.P. Filatov (1943) called them the form developing apparatus, in the history of individual development and in the evolution - the problem of experimental embryology, was solved by the method of comparative experimental investigation. It is practical to reveal the formative action of one rudiment on the other by means of enzymatic or hormonal factors can be done only experimentally. However, the displacements in these morphogenetic correlations in the evolutionary development can also be discovered and their biologic importance can be understood on the basis of comparative-embryologic studies for a number of related forms, distinguished by different ecological conditions.

Comparative-embryologic studies of the transformation of cuti in vertebrates in the series from lower groups to upper (B.S. Matveyev 1930, 1932, 1940, 1945 and 1949) opens ways for phylogenetic study and the

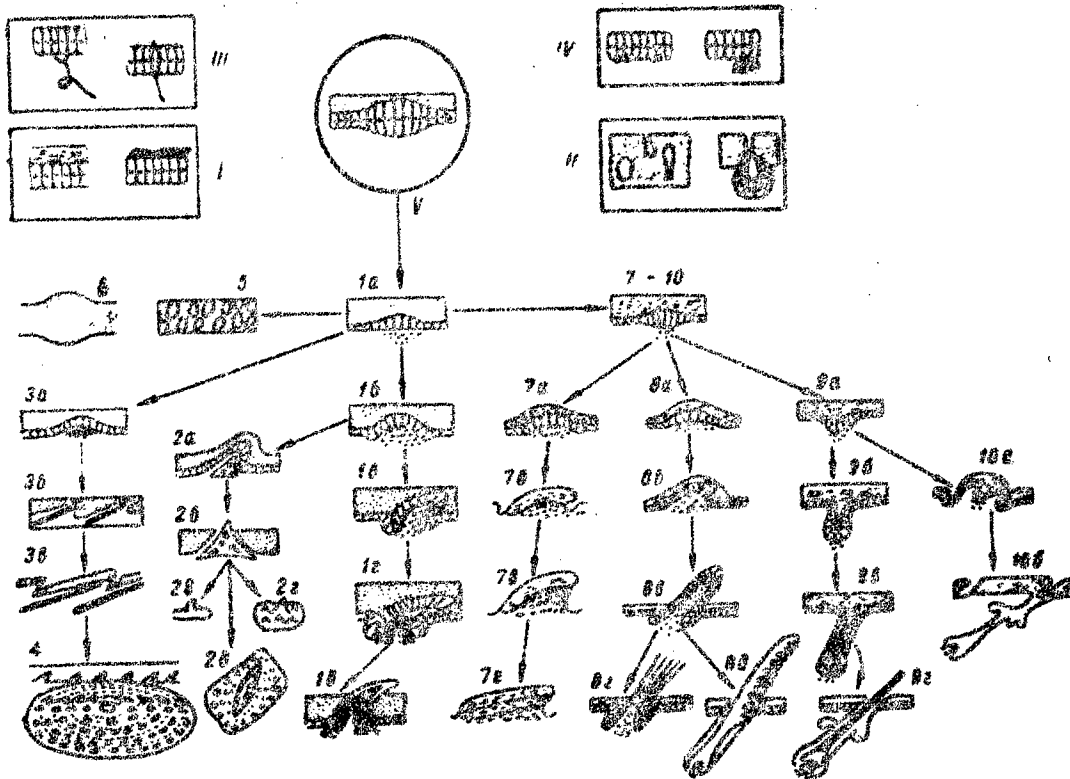


Fig. 2. Scheme of the evolution paths and trends of ontogenetic differentiations of the cutaneous covering for vertebrates in phylogenetic development.

I-V - Function types of cutaneous coverings: I - Protective

(by forming cilia and cuticles); II - Secreting (by forming single cell and many cell glands); III - Sensing (by separating the primary and the secondary sensory cells); IV - Coloring (by differentiatinal pigment cells); V - Embryonic laying of protective skin organs in vertebrates by forming the form development apparatus. 1a-1b - Number of stages of dentine formation in sharks (Selachii) with the formation of placoid scales with a typical enamel organ; 2a-2b - Development of bone denticles (2a-2b), dorsal "zhuchek" and end plates (2c-2d) in the skin of sturgeons (Acipenseridae) with the dropping of dentine formation; 3a-3c - Development of cycloidal scales in the skin of bony fish (Teleostei) with a complete rudimentation of the enamel organ; 4 - Diagram of the ganoid scale, as an example of a complex of many scale generations; 5 and 6 - Replacement of skeletongenetic function by glandular function in fish skin; 7-10 - Common rudiment of horny scales, feathers and hair in amniots; 7a-7d - Developmental stages of horny scales in reptiles and birds; 8a-8d - Development of downy feathers and 8e - Development of contour feather; 9a-9d - Development of hair stages with complete rudimen-

tation of connective tissue and the developmental progress of the epidermal rudiment; 10a-10b - Restoration of horny scales in mammal skin.

transformation of cutaneous coverings in mammals and conclude that it occurs in successive ontogenetic series by displacement of morphogenetic correlations between the epidermal organ rudiment and its mesodermal part, developed in the coelium. These displacements occur under the influence of the rudimentary function change of cuti, depending on the developmental conditions. A table in diagram form is given on Fig. 2 which illustrates the transformations of cutaneous covering organs in embryonic development. It should be remembered, that the cutaneous covering is a system of organs, which has a well-expressed multi-functional character. For most animal species the presence of four groups of cutaneous covering functions is characteristic: Protection (I), secretion II, sensitivity III and coloring IV, which are in close dependence on each other. Let us turn our attention to the protective function, which is expressed in the vertebrates by the development of

different scales and their derivatives - feathers and hair, and also of the cutaneous skeleton. In all vertebrates in their ontogenetic evolution is the primary rudiment, formed by the concentration of cylindrical cells of the epiderm growth layer (V). This ectodermic placoid interacts with mesenchymal cells and forms the apparatus of "form development", as D.P. Filatov understood it, where placoid epidermis is the activator and mesenchymal rudiment is the reactor, at the expense of which the "form development" of skeletal elements takes place. As the data of comparative anatomy and paleontology show, the earliest and primary process in vertebrates is dentine formation, i.e., the development of dentine denticles in the skin according to the type of placoid scales in present-day sharks and teeth in the mouth (see Fig. 2, 1a to 1d). The placoid epidermis transforms into the enamel organ, which produces dentine formation through the transformation of mesenchymal cells into odontoblasts. At present after a long discussion among paleontologists and morphologists on the problem of the origin of external bony skeleton in early lower vertebrates we can assert, that the skin armor of the

early agnathous (Agnatha), placoderms (Placodermii), bottom-dwelling cartilaginous fish (Chondrichthyes) and early bony fish (Osteichthyes) was formed through the transformation of primal dentine scales into cosmoid, ganoid scales and bone shields (see Fig. 2,4). In the most of the present bony fish (Actinopterygii) the ability of dentine formation was lost. The skeleton formation character in the mesenchyme papilla depends on the degree of enamel organ development which in turn depends on the condition of the skin secretory function. By increasing the function of mucous separation the formation of enamel organ in the epidermis is stopped, and it disintegrates. As a consequence of this the morphogenetic mutual relation of the enamel organ and mesenchyme papilla is disrupted, and bone is formed instead of dentine. The ability of dentine formation is preserved in the mouth where dentine teeth develop, in other coatings however it is replaced by bone formation. This can be well seen from the development of the bony scales in sturgeons (Acipenseridae). Sturgeons maintain the ability to develop many scale generations as the sharks do, but

instead of dentine denticles, bone denticles develop in their skin. The development begins by a formation of typical ectodermal placoids (see Fig. 2, 2a to 2e), from which the rudimentary enamel organ is formed, but it rapidly disintegrates still before the beginning of skeleton building. In the mesenchyme papilla, osteoblasts appear and bony dentines develop (B.S. Matveyev 1940). By way of growing together of separate bone dentines in different generations and their further development, characteristic longitudinal series of "Zhuchek" form with star end-plates between them. Further underdevelopment of ectodermal placoids in bone fish (Teleostii) causes a further change in the scale development. The enamel organ rudiment has been discovered by me in bony fish in rudimentary state in the earliest stages of scale development, and this immediately disintegrated. In addition to this mutual interaction of epidermis and chorium was noted. The placoid ectodermal rudiment appeared only when the peeling of epidermis from chorium occurred. As soon as the enamel organ rudiment originates in the form of the thickening of the epidermal basal layer (Fig. 2, 3a to 3c), a concentration of scleroblastoma

occurs under it and a thin plate of osteoid tissue, without bony bodies is formed. The placoid ectodermal rudiments of the enamel organ begin to separate in the basal epidermal layer, when the skin reaches a specific differentiation level, which depends first of all on the developmental stage of the embryo and, moreover, on the degree of mucous section development. The sequence in scale rudiment distribution depends on different degree of skin differentiation on different body sections. It is interesting to note the differences in the differentiation level of epidermis as the external coating from the influence of external medium factors in relation with different way of life of the young. Thus, in the fry of the naked dyptichus (Dyptichus dybowski), living in a protected environment, the epidermis reaches a considerably lesser vigor, than in the fry of the scaled dyptichus (Dyptichus maculatus), living in fast current conditions, leading a bottom-dwelling form of life on stony bottoms, and so on. Corresponding to this, we see a lag of scale coating development in the first ones, and sometimes its complete reduction. In the second ones, on the other

hand, an earlier scale development and their progressive development are noted.

Still a more complicated reconstruction of interaction between ectodermic and mesenchyme scale rudiments and their derivatives occurs in Amniota (reptiles, birds and mammals) in relation with the sclerosing of the skin coatings. The replacement of mucous section by horn formation creates the development of skin organs (Fig. 2, 7 to 10). Rudiments of horn scales, feathers and hair appear in the epidermis still before the beginning of sclerification, and possess the characteristic form of placoid ectodermis and the accumulation of mesenchyme cells under it (Fig. 2, 7 to 10). With a larva type of development the formation of scales and other skin covering organs occurs in the three way of living, when the developing organism collides directly with the external medium and all the diverse functions (secretion, breathing, protection, sensation, and color) are of great biologic importance. With oviparity and viviparity when development occurs to a considerable degree in indirect relation with external medium, most of the functions, except sensitivity, lose their biologic meaning. The

development of horny scales, feathers and hair takes place in completely different conditions. In fish the epidermal placoids play the role of functioning enamel organ only for a short time, and predominant value in the development falls on the mesenchyme part, where different forms of skeletogeny are accomplished. In all Amniota however, a predominant value goes over to the epidermal establishment and the connective tissue part in the form of a pulp in the majority carries only the function of providing the nutrition. In reptiles (Fig. 2, 7a to 7c) the rudiment preserves the form of a scale-shaped organ, although the scale itself (with connective tissue papillae inside) develops from the epidermis. However, as it is known, in many reptiles the ability to develop bony formations is maintained, and bony plates under bony scales form in different groups (turtles, crocodiles, chameleons, gekos, etc.) independent of one another. In birds the development of scales and feathers begins in a fashion similar to that of the development of scales in reptiles, in the form of scaly organ rudiments, and typical horny scales are developed on the legs. On the body

however, the development does not stop with the condition of a scale-shaped rudiment, but transforms into a papilla-shaped organ with further disintegration of epidermal cap into longitudinal threads of the feather (Fig. 2. 8a to 8b). With the development of hair in mammals only the very earliest rudiments have the form of ectodermal placoids (B.S. Matveyev 1932 and 1949), and then the epidermal rudiment reaches complete dominance, and the mesodermal part has a subordinate role in the form of a hair bulb (Fig. 2, 9a to 9d). However, the ability to form scales is potentially maintained, and independently in different mammalian orders scaly covering develops on the tails and claws (Fig. 2, 10a to 10b).

The third group of factors, which influence the morphogenetic characteristics and the origin of neoplasms in ontogeny is the change of organ functions in relation with the transformation of form and metabolism in different periods and the stages of individual development, corresponding to the organizational level on the given segment of individual development, and new relationships to the environment. According to the indication of

Darwin, recorded in the essay of 1844 "Selection in the course of successive centuries continues to adapt horns to some single purpose and larvae - to an entirely different purpose, therefore it is not surprising that the differences between them are strikingly great... and if the embryonic form should search food for itself, then its structure and adaptation will be as important for the species as the structure and adaptation of the adult organism" (Essay 1884, Works, Vol. 3, 1939, page 214).

A.N. Severtsov further developed this point of view in "Studies on the theory of evolution" (1912) he wrote: "The function of organs, and consequently their morphologic and histologic structure, are adopted and coordinated not only to specific environments, but also to the specific life stages, respectively; 1. General structure of the animal at a given age and 2) corresponding to conditions of external medium, in which it lives in this stage" (Works, Vol. III, 1945, page 101). Soviet morphologists V.V. Vasnetsov, S.G. Kryzhanovskiy, B.S. Matveyev, Mashkovstev, S.N. Bogolyubskiy, G.A. Shmidt and their pupils, continued the development of these problems along different paths. This area of

evolutional embryology is most interesting for comparative eco-morphologic studies. When studying the transformation of adaptations related to the search of food V. V. Vasnetsov (1946-1953) developed the problem of stages for individual development of fish, G.A. Schmidt (1953-1955), S.M. Bogolyubskiy developed the problem of periodicity in embryonic development in animals. These problems are of great importance in artificial breeding of animals, and they are extensively developed by specialists, practical workers in fish culture, poultry and cattle-raising.

Unfortunately morphologists and theorists of evolution in foreign literature give insufficient attention to problems of function transformation in ontogeny. Thus, for example, A. Remane (1956) in his thorough summary, concerned with "Principles of the natural system, comparative anatomy and phylogenetics", in the survey of biogenetic law and phylogenetic changes of ontogeny gave a very detailed analysis of different presentations on this problem, but completely omitted the transformation of functions. The problems of change in life, change and the expansion of functions were analyzed by him in

relation with specialization laws, and in relation with paleontological data, but aside from the rules of individual development. B. Rensch (1954) in his excellent summary "New problems of evolution" with many-sided analyses of the methods of "nadvidovoy" (trans-specific) evolution came to an important conclusion on the absence of independent beginnings as moving forces of evolutionary development. When analyzing the cladogenesis rules, i.e., the phylogenetic divergence of species, he gave much attention to phylogenetic transformations of ontogeny in its different stages. However, B. Rensch limited himself to the review of different deviation modes, without broaching the rules of functional transformations. At the same time Darwin attached great significance to transition methods from one form to others. I will recall what he wrote: "We should observe extreme care in concluding that this or another organ could not form by means of a number of transitional stages. Many examples could be given that one and the same organ simultaneously performs completely different functions in lower animals; further, two different organs or one and the same organ

in two different forms can perform at the same time in the same species, one and the same function, and this represents an extremely important transition method", "Origin of the Species", (Works, Vol. III, 1939, page 405). A. N. Severtsov in the book "Evolution and Psychology" (1923) emphasized that "aside from hereditary organ changes there are also behavioral changes in animals without change of their organization, which plays an important role in the process of evolution and serves as an important means of animal adaptation to environment".

It is impossible for me in this article to dwell on the natural regularity of function transformation rules in relation with changes of environment. I just wish to note again, as I often have (B.S. Matveyev 1939, 1940, 1953 and 1957), that all function transformation rules in phylogenetic development (A.N. Severtsov 1931 and 1939) even more descriptively proceed in individual development. More than that, it seems to me, that by studying the role of ontogenetic transformations in adaptive evolution there could be the formation of species and in control of development with the formation of races. At

the present time we cannot be limited by a problem of when and how the ontogenetic change originates. It is necessary to reveal the causes of the originating changes. In the chain of transformations in the developing organism, inherited from ancestral forms, in relation with the changes in habitat conditions, the function transformations are included, which in successive order of generations lead to transformation in the structure or organs. As it was correctly noted by V. Vasnetsov (1946 to 1953), in each stage and period of individual development, a qualitative change of functions occurs, and corresponding with this also occurs the qualitative level change of organization and biology.

The transformation analysis of the breathing function gives us a very elucidating example of function transformation in ontogeny. Still in 1934 S. Kryzhanovskiy noted the replacement of provisory breathing organs in the development of fish. Breathing in the course of individual life of the organism remains one and the same - providing oxygen for all organs, in distinction from feeding or a numerous replacement of food objects there

occurs, therefore, the transformation of different forms of one and the same function descriptively seen in the breathing process. In the early developmental stages of fish, the embryo breaths through the whole surface of the body (osmotic breathing), then the breathing function is accomplished by a grid of blood vessels on the vitelline sac. The breathing by vitelline blood circulation is gradually replaced by jaw fringes on the hyoid and mandible arches (external mandible breathing), frequently in addition to them a capillary network of vessels develops in the unpaired fin edge. Only at the end of the larval period the definitive opercular-mandible breathing act enters into action. Thus, before the beginning of the functioning of the definitive jaw in the embryo a whole number of provisory breathing organs pass replacing each other in succession. Before us is an example of the phenomenon of organ substitution, performing the breathing function, and simultaneously the function substitution in organs, providing the breathing for embryo and larva, in the definitive state however, performing completely different functions (B.S. Matveyev

1940 and 1957).

We will discuss the role of organ function transformation in ontogeny, as a factor, which influences the morphogenetic character, also by an example of the development of skin covering organs. Skin coverings are systems of organs, possessing the most clearly expressed multi-functionality, whereupon all function changes in these organs are directly related to the animal's mode of life and the environment. For the epidermis, besides the above-stated inducing function of skeleton building, glandular function is extremely characteristic. The comparative embryologic studies of fish skin development show that these two functions are in an antagonistic to each other. The function of skeletal induction is dependent on the intensity of glandular function, the stronger is suppressed (B.S. Matveyev 1945). Before us we have an example of phylogenetic organ change, which is called function substitution (A.N. Severtsov 1931). Skin skeleton and mucous section accomplish the same function protection of animal's body from external influences, but in different ways. With hypertrophy of glandular function,

the skeletogny function can completely fall out (Fig. 2, 5 to 6). Indeed we see that forms, for which a strong development of mucous section function is characteristic, possess a bare skin, the skeleton formations in them are reduced. Besides this it is interesting to note that the ability to form skeletal formations is not completely lost either in future ontogenetic development nor in phylogeny, and in cases of the glandular function weakening it can be restored again, if this will be useful to the animal.

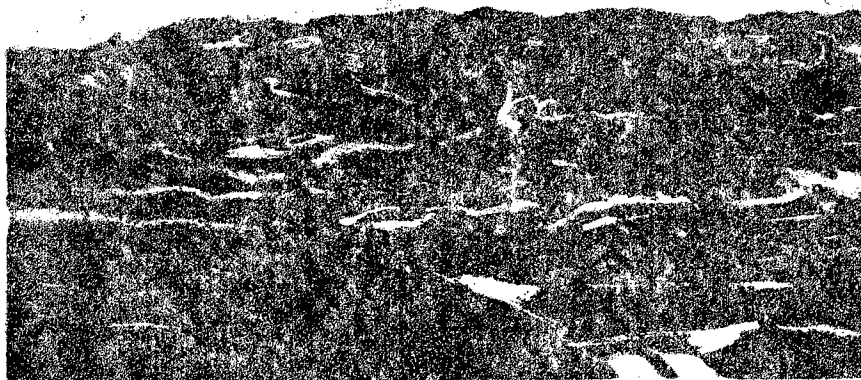


Fig. 3. Skin cross-section of catfish fingerlings (Callichthys) 19 mm long with enamel organ rudiments.

Microphoto.

As an example we will discuss the relation between glandular and the skeletal-building functions in the skin

of catfish. As it is known, for a number of catfish (Siburidae, Amuridae) the presence of bare skin is characteristic, and for armored catfish (Callichthyidae, Loricariidae, Trychomycteridae), besides the presence of bony armor, the presence of real placoid hooks is characteristic on the external surface of the bony armour plates. The studies of O. Hertwig (1876 and 1979), G. Klaatsch (1890), Aykheh (1916), Payer (1928) and others established complete structural homology of dentine forms in armoured catfish with placoid scales. Study of their development (Bati-Hamid-Kan 1938) in catfish (Callichthys) fully confirmed the histologic studies of other authors. To explain the above-raised problems on the effect of mucous secretion function on the skeletal-building function, I undertook the comparison of skin development of the catfish (Callichthys) and of (Silurus glanis).

In the catfish the development of two scale generations is maintained. In early stages the bony plates are established, which form bony shields of the external armour, and considerably later the second generation of scales is formed, which developed as typical placoid scales

with an enamel organ, dentine and enamel. Skin cross-section of 19 mm length catfish fingerling is illustrated in Fig. 3. In this stage we find the first scale rudiments. They lie correctly segmentally opposite each myocomma. The epidermis in this stage is thin and almost deprived of glandular function. The presence of three layers of epidermal cells on the average and only three glandular cells on the whole segment are seen in the cross-section. Opposite myocomma the establishment of enamel organ with a dentine cone rudiment is seen, and under the enamel organ independently lies the accumulation of scleroblasts, forming the osteous bony plate. These bony plates are developed according to the type of cycloidal scales of bony fish and by growing form bony shields of the external armour in catfish. In later developmental stages in 29 to 35 mm fingerlings a second generation of scales is developed external to the bony plates of the external armour in the form of separate dentines, which later adhere to bony shields. Second generation of scales is developed when the epidermis becomes multi-layered and by its thickness suggests the epidermis of sharks. In

In relation with this with the development of second generation of scales, a real enamel organ is formed and a typical placoid scale with dentine is developed (bhati-Hamid-Kahn 1938).

In 79 to 80 mm bare catfish (Silurus glanis) the development of skin proceeds in another direction. In Fig. 4 three cross-sections in different places of the body are represented (belly, tail section and fins), illustrated with one and the same magnification. In all cross-sections the epidermis is many-layered, i.e., by its differentiation it is considerably older than in catfish, but there are no bony formations either on the belly (Fig. 4 a) or on the tail (Fig. 4b). On the other hand, there are many gland cells, indicating on the highly-developed glandular function. The large flask-shaped gland cells and the mucous cells are distributed in two to three rows on the belly. In the tail section, where the moving function of the body is more developed the number of mucous cells is considerably smaller (1-2 rows). On the cut through the back fin (Fig. 4 c) the mucous function of epidermis is almost absent on both

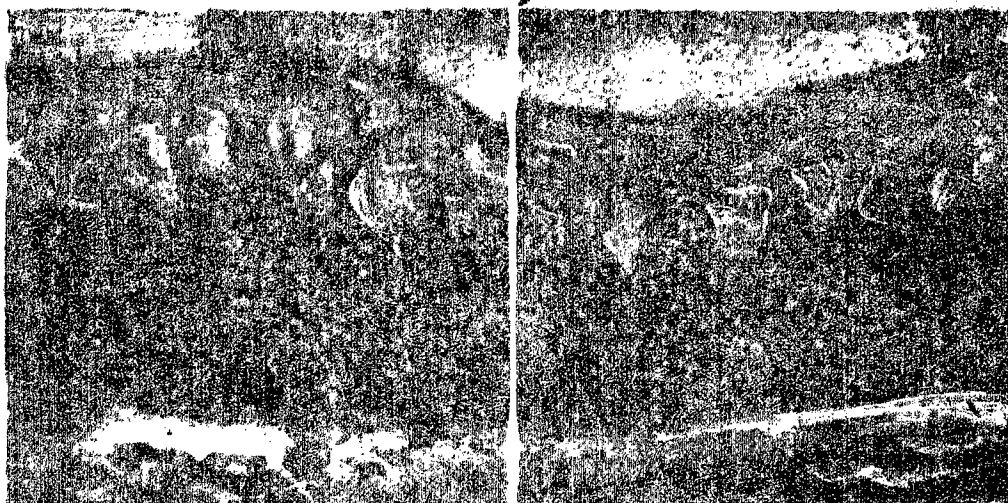


Fig. 4. Skin cross-section of 79 to 80 mm long bare catfish (Silurus glanis).

a - on the belly; b - on the tail; c - through the back fin. Microphoto.

sides of the fin. Only separate gland cells are seen on the cross-section, whereas under the epidermis the bony plates of lepidotrichia lie in the connective tissue. The comparison of these three sections gives a clear picture of glandular and skeletal skin function interaction. The skeletal function in catfish is completely replaced by the mucous excretion function.

But the skin does not lose the ability to develop bony scales. The whole body of catfish remains bare, but on those sections of the body, where the adenoblasts are few, the epidermis essentially maintains the skeletogeny function. Thus in a one year old catfish (150 mm), caught by L.S. Berg in the Amu-Dari and given to MGU Zoological Museum, we discovered several scale-shaped rows on the gill cover external to its bony plate with complete absence of scales on the whole body. The skin cross-section on the gill bar of this catfish is illustrated in Fig. 5. The epidermis is here many-layered, on the cut there are found adenoblasts but there are also typically-developed scale establishments with a well-developed enamel organ in the form of Malpighian epidermis

layer gala. Under it by using Mallory's stain we see bony galas, which are stained with blue, reminiscent of the dentine cones of placoid teeth. Thus, the bare skin of catfish (Silurus glanis) did not lose the ability to form skeletal formations the skeletal-building function being only suppressed by glandular function. Before us we have an example of a phenomenon noted by Darwin: when the descendant keeps the hereditary transmission at the corresponding age the ancestor sign, inherited by the descendant, can for a long time be in a latency and will appear only in the following generations. The appearance of a latent sign in the following generations occurs, when it becomes a useful adaptation in its relation to environment.

According to the law of hereditary sign transmission in the corresponding age (Darwin), fish skin eventually preserved the possibility to form placoid scales, but this potential is latent. Only in the mouth of the vertebrates the endodermal covering realizes this potential in the form of the tooth system. In some fish, for example, in the armoured catfish, this potential was

again restored with the development of bony armor as an adaptation to protection from enemies.

Fig. 5. Skin of 150 mm naked catfish (Silurus glanis) in the region of the gill cover. The establishment of the enamel scale organ is seen. Microphoto.



A similar realization of the latent skeletogeny potential was restored on the gill cover of the bare catfish in the second year of its life. Before us is an example of the restoration of the lost correlative interrelations of chorium and epidermis as two parts of form developmental apparatus for the development of scales in those skin sections where the skeletogeny epidermis function could have been restored due to the weak development of

adenoblasts.

Similar kinds of effects of distant ancestor sign restoration in the descendent, lost in the ontogeny of the closest relatives, were named by me secondary recapitulations (B.S. Matveyev 1929). The fact of placoid scale restoration in the skin of catfish is a new example of secondary recapitulations.

The establishment of the fact of preservation in latency of an old ancestral sign and the possibility of its restoration in the ontogeny of present descendants with a change of relationship in its functions and depending on the environment present a great interest in another respect. If we meet restoration cases of an old sign with the change of function in the natural environment then this gives a right to the biologist to work at the restoration of latent signs in experimental conditions. If this were successful, then the biologist would have the possibility of directing the development of animal breeding according to his own judgement and to open potential possibilities in ontogenesis which can be used by a man for his own needs.

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Author's address: Moscow, K-9, ul. Gertsena, 6, kv. 21.

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